

**BIOLOGY OF *ILYTHEA CANICEPS*, *I. SPILOTA*,
AND *ZEROS FLAVIPES* (DIPTERA: EPHYDRIDAE),
CASE-MAKING CONSUMERS OF DIATOMS ON SHORELINES**

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Abstract.—Life history information is presented for *Ilythea caniceps* Cresson, *I. spilota* (Curtis), and *Zeros flavipes* (Williston) (Diptera: Ephydriidae). Adults of all three species were commonly encountered along shorelines of small streams that possessed moist to wet substrates, where adults deposited eggs. The incubation period lasted two to three days. Larvae consumed a mix of pinnate diatoms. Newly hatched larvae formed a protective case by affixing a mix of sand grains and detrital particles to their dorsal surfaces. The larval period lasted 8–10 days. Puparia were formed in the same habitat occupied by the larvae. The dorsal cases formed by the larvae remained in place on the upper surface of the puparia. The pupal period lasted 6–10 days. All three species were multivoltine.

Key Words: Diptera, Ephydriidae, *Ilythea*, *Zeros*, life histories, larval feeding habits

Shore flies of the family Ephydriidae occur in nearly all of the world's biotic regions and consist of nearly 1800 described species, as well as a host of undescribed taxa (Mathis and Zatwarnicki 1995). It is the second largest family of acalyptrate Diptera in the Nearctic Region, consisting of over 460 species in 71 genera. Phylogenetically, the family is considered to be particularly close to the Risidae, and both families are currently placed in the superfamily Ephydroidea along with the Camillidae, Diastatidae, Campichoetidae, Drosophilidae, and Curtonotidae (Grimaldi 1990).

Knowledge of the biology and ecology of the Nearctic species of Ephydriidae is weak but improving (Deonier 1979, Foote 1995). Information is particularly extensive for those species that occur in more unusual aquatic habitats. For example, life history studies of species of

the tribe Ephydrini that are found in alkaline or saline lakes and ponds and in thermal springs are fairly numerous, but relatively few studies have focused on the numerous species of the family that occur in less exotic habitats (Foote 1995). Overall, probably no more than 25% of the Nearctic species of Ephydriidae have been investigated with respect to their life cycles and larval feeding habits. Knowledge of the morphology of the immature stages is even less extensive, and probably less than 10% of the larvae of the North American species have been described. In agreement with those of the Drosophilidae, most ephydrid larvae are basically microphagous in feeding habits, with microorganisms and finely divided particulate matter serving as the nutrient base. However, in contrast to the yeast-feeding habits of the drosophilids, larvae of some ephydrid

taxa commonly ingest algal cells (see references in Foote 1995, Keiper et al. 2002). Another biological difference in the two families is the occurrence of Drosophilidae in shaded forested habitats, whereas species of Ephydriidae are most commonly encountered in open wetland sites where autotrophic microorganisms are abundant.

Ilythea, *Zeros*, and *Donaceus* are the only genera belonging to the tribe Ilytheini (Ilytheinae) (Mathis and Zatzwarnicki 1995). The genus *Donaceus*, consisting of two species, is Oriental and Afrotropical in distribution and unknown biologically. *Ilythea*, with 12 species, has a Holarctic, Neotropical, and Afrotropical distribution, whereas *Zeros*, with 11 species, occurs in the Holarctic, Neotropical, Afrotropical, and Oriental regions. The Nearctic Region contains three species of *Ilythea*. *Ilythea caniceps* Cresson has been recorded from California, Oregon, and Washington south into Mexico and Costa Rica, *I. flaviceps* Cresson is known only from Arizona and California, and *I. spilota* (Curtis) has a transcontinental distribution in North America and also occurs in the Palearctic Region. The genus *Zeros* has five species in North America. *Zeros calverti* (Cresson) and *Z. fenestralis* (Cresson) are known only from Florida in the Nearctic Region but also occur in the Neotropical Region, *Z. flavipes* (Williston) is widespread in the eastern states and Canadian provinces and also occurs in the Neotropical and Afrotropical Regions, *Z. obscurus* (Cresson) has been recorded only from Arizona and New Mexico and from the Neotropical Region, and *Z. vicinus* Cresson occurs only in Florida in North America but also has been recorded from the Afrotropical Region.

Little has been published on the biology of any species of the tribe Ilytheinae, and no larvae or puparia have been described. The egg of *Z. flavipes* was

illustrated by Scheiring and Connell (1979) who reported that eggs are inserted into moist soil. They suggested that the slender filament arising from the dorsal surface of the egg serves as an aeropyle (Hinton 1968). Foote (1995) reported that larvae of *Ilythea* and *Zeros* consume diatoms.

This paper presents information on habitat occurrence, larval feeding habits, case-building behavior, and general life history of *Ilythea caniceps*, *I. spilota*, and *Zeros flavipes* whose larvae consume diatoms in shoreline habitats. The biology of the three species is contrasted and compared with that of other species of Ephydriidae having larvae that feed on diatoms, and resource partitioning within this guild of diatom-feeders is discussed.

MATERIALS AND METHODS

Field work for this study was carried out in northeastern Ohio near Kent in Portage County between 1982 and 1996, and in southern Arizona in 1970–1971. Habitats studied included riffle rocks in small woodland streams, gravelly, sandy desert streams, and muddy shorelines. Pairs of adults obtained by sweep netting in nature were established in small breeding jars (5.5 × 7.0 cm) containing substrate taken from the habitat. Eggs obtained from these pairs were either allowed to hatch on the field-collected substrate or were transferred to large Petri dishes containing a monoculture of diatoms (*Navicula pelliculosa* (Bréb.) Hilse) growing on nutrient agar (Zack and Foote 1978).

RESULTS AND DISCUSSION

Life History of *Ilythea Caniceps*

Rearings of this species were initiated on 12-V-1971 from a gravid female collected along a small, intermittent stream in Upper Sabino Canyon near Tucson, AZ (32°19'19"N, 110°48'35"W).

Additional rearings were initiated with larvae collected in a sandy substrate along the same shallow stream on 20-V-1971. Other ephydrid adults collected at the same site included *Lytogaster excavata* (Sturtevant and Wheeler), *Pelina* sp., *Athyroglossa* sp., *Discocerina obscur-ella* (Fallén), *Parydra appendiculata* Loew, *Scatella laxa* Cresson, *S. marinensis* (Cresson), and *S. paludum* (Meigen). The sand shore was moist to wet and had a distinct yellow-green cast due to an abundance of algae, including large numbers of diatoms. Examination of the gut of one adult showed that it had ingested diatoms.

Four eggs were noticed on V-15 in the sand substrate in the breeding jar. They were placed horizontally in the moist sand and had a distinct elongate stalk at midlength that extended into the overlying air. Hatching began that evening when one larva was discovered moving slowly over the sand substrate. It had a distinct hump-backed shape and continuously moved its mouthparts in a flickering motion. Within an hour of hatching, I noticed that the larva had formed a case composed of sand grains and small detritus particles that covered its dorsal surface. The case retained its shape when removed from the larva, and the particles appeared to be glued together by a secretion released by the larva.

On V-20, six third-instar larvae of *I. caniceps*, 12 larvae of a species of *Lamproscatella*, 6 larvae of at least 2 species of *Scatella*, and numerous eggs of *Parydra appendiculata* were collected at the same site. All of the *Ilythea* were distinctly hump-backed and possessed dorsal cases composed of sand grains and detritus. The integument appeared to be distinctly thinner in the area covered by the dorsal case. The larvae moved about on the moist sand rather swiftly while exhibiting the flickering movement of the mouthparts. I removed

the dorsal case from one of the larvae and noted that it immediately gathered up small particles from the substrate and reformed the case within a few minutes. Larvae moved about on the surface of the moist sand but did not burrow down into it. The gut on one examined larva was filled with a mix of pinnate diatoms belonging to the genera *Navicula*, *Stauroneis*, and *Synedra*. No non-diatom algal taxa were noted in the gut, suggesting that this species is a specialist on diatoms.

On V-24, numerous eggs, and at least 16 second- and third-instar larvae were found in a Petri dish-sized sample (area of 64 cm²) taken near the center of the sampling site that was about 3600 cm². The larval period varied from 5 to 10 days (5 larvae).

Puparia were formed in the same area where larvae occurred and all retained the dorsal case. The pupal period lasted 9–10 days (4 puparia).

Life History of *Ilythea Spilota*

Adults of this species were most commonly encountered in shoreline habitats that contained large populations of pinnate diatoms. Numerous specimens were also collected from various-sized rocks that projected above the water line in riffles of small woodland streams. Interestingly, habitats that were open to sunlight did not contain larger populations of *Ilythea* than sites that were partially or mostly shaded. In fact, populations frequently were comparatively larger in shaded habitats than in the more open areas of the shoreline or riffle. Deonier (1965), in a study of ephydrid habitats in Iowa, reported that *I. spilota* was most commonly encountered in the stream-rock habitat, although it was found also in the limnic-wrack, sedge-meadow, and muddy-shore habitats. In contrast, Scheiring and Foote (1973) collected adults most commonly on muddy shores, with fewer

recorded from limnic-wrack, grass-shore, rain-pool, and marsh-reed habitats. Results similar to the latter paper were obtained in Scandinavia by Dahl (1959) who reported that the center of ecological distribution for adults of this species was the mud-shore biotope, although he also regularly encountered them in moist meadows and over wrack deposited on high beaches bordering freshwater lakes.

This is a multivoltine species, and adults are repeatedly collected throughout the warm season in northeastern Ohio. The first specimens were obtained on April 15, and the last on October 2. Populations were particularly large in mid and late summer once stream flows stabilized and diatom populations surged. As reported by Deonier (1972), adults fed on pinnate diatoms. Guts of field-collected adults of both sexes contained nearly pure cultures of diatoms with only occasional cells of other algal taxa. There was no obvious trophic separation between adults and larvae, as similar diatom taxa were found in both life stages.

A male and female collected in a stand of skunk cabbage (*Symphoricarpos foetidus* (L.) Nuttall) along the Cuyahoga River in Kent, Ohio, was placed in a Petri dish supporting a pure culture of *Navicula* diatoms on 20-VIII-1976. Adults fed on the lawn of diatoms, as numerous areas cleaned of cells were noted. Six eggs were laid on August 23. All were placed horizontally in the layer of diatoms and all supported an upright stalk at mid-length. Hatching began on VIII-24, giving an incubation period of 1–2 days. The larvae fed steadily on the monoculture of *Navicula* and all formed dorsal cases of diatoms. Larval feeding ended on IX-02, giving a larval period of 8–10 days ($n = 5$). The dorsal cases remained in place on the upper surface of the puparia. The female died on IX-06, having lived for 17–18 days in the

Navicula culture. Adults emerged from the 5 puparia on IX-08 and IX-09, giving a pupal period of 6–7 days. Three of the emerged adults (2 males, 1 female) that were transferred to a fresh plate of *Navicula* on IX-13 began laying eggs on IX-23, giving a pre-oviposition period of some 10 days.

Several larvae were collected from a muddy, diatom-laced shoreline of Cave Creek in the Chiracahua Mountains of southeastern Arizona on X-23-1976. All larvae bore dorsal cases composed of diatoms and detrital particles, although one larva had attached an empty *Ilythea* egg shell, and another had affixed a small, dead larva to the case. Gut examinations of two third-instar larvae disclosed a nearly pure culture of pinnate diatoms belonging to several undetermined genera.

Numerous collections of adults and immature stages between late May and early October in northeastern Ohio indicate that this is a multivoltine species. With an incubation period of 2–3 days, a larval period of 10–13 days, and a pupal period of 6–10 days, there could be as many as 7–8 generations produced during a warm season of some 180 days in this latitude and longitude.

Life History of *Zeros Flavipes*

The single rearing of this species was initiated from a gravid female collected on VIII-13-1976, from the sandy/muddy shores of the Cuyahoga River in Kent. She was placed in a large Petri dish that contained a monoculture of the diatom *Navicula pelliculosa*. By VIII-15, she had scattered eight eggs over the diatom culture, with each egg being buried horizontally in the agar except for the upward-directed projection arising at mid-length on the dorsal side of the egg. The incubation period of the eight eggs was two days. The female died on VIII-16, although numerous eggs were still visible within her abdomen.

The six newly hatched larvae moved slowly over the surface of the diatom culture and quickly began ingesting diatoms, as shown by the yellowish material that appeared in the gut. All larvae constructed a dorsal case of diatoms and egg shells within one day of hatching. Larvae continued to feed on the diatom culture, with the first stadium lasting three days ($n = 6$); the second, two days ($n = 2$); and the third stadium, five days ($n = 1$). The total larval period from hatching to pupariation in the single larva that formed a puparium was nine days. The dorsal case was reconstructed after each of the first two molts and remained in place over the puparium. A male emerged on VIII-31, giving a pupal period of 6 days ($n = 1$).

Another gravid female was collected on IX-01-1982 near the original collecting site. She was associated with the shore flies *I. spilota*, *Athyroglossa granulosa*, and *Scatella picea*, but deposited no eggs during the 14 days she was held in a Petri dish containing a monoculture of *Navicula*. This collection was interesting in that it showed that both *I. spilota* and *Z. flavipes* can co-occur in the same habitat.

Undoubtedly the most interesting and distinctive behavior of the larvae of these two genera was the repeated construction of a case that covered their dorsal surfaces. Case building began almost as soon as larvae hatched, was maintained through all three larval instars, and remained in place on the dorsal side of the puparium. When I removed the case, the larva quickly began the construction of a replacement. Because the construction of a dorsal case requires an energy expenditure, it appears that there is selective value in its construction, and at least two possible roles of the case can be suggested. Because the larvae crawl about on exposed surfaces (mud, sand, rock), there is high likelihood of con-

tacting predators such as larvae of Hydrophilidae (Coleoptera) that are common in such habitats. Therefore, it is possible that the case serves a protective role in that it serves to camouflage the feeding larva. The integument of larva appears to be quite thin under the case, and it is possible that the case shields the larva from ultra-violet radiation, prevents overheating or retards desiccation.

One interesting puzzle is how the co-occurring larvae of two or more species manage to avoid competition, assuming that there is a limiting resource. This was not explored in this study, but it is quite possible that there is some microspatial segregation of the feeding larvae. For example, larvae of one species could occur on somewhat drier surfaces, whereas the second species occurs more commonly on wetter surfaces. Of course, there is also the possibility that there is no limiting resource (diatoms) because larval populations are relatively low.

The utilization of diatoms by ephydrid larvae is particularly well developed in these two genera and in species of *Parydra*, and all commonly co-occur in diatom-rich habitats. One interesting difference in the feeding of *Parydra* larvae (Deonier 1978) versus that of the larvae of *Ilythea* and *Zeros* is their mode of segregating diatoms from the substrate. There is no indication of pharyngeal ridges in the mouthparts of *Parydra*, but they are present in larvae of the other two genera. It has been shown that pharyngeal ridges serve as a filtering device in particle-feeding larvae of acalyptate larvae (Ferrar 1987), but the mode of filter-feeding in *Parydra* larvae remains unknown.

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